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Establishment of salmonberry, salal, vine maple, and bigleaf maple seedlings in the coastal forests of Oregon[1]

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To identify seedling regeneration niches for four coastal Oregon shrub and hardwood species (salmonberry (*Rubus spectabilis* Pursh), salal (*Gaultheria shallon* Pursh), vine maple (*Acer circinatum* Pursh), and bigleaf maple (*Acer macrophyllum* Pursh)) we studied the seed predation, emergence, survival, and growth of these species on disturbed and undisturbed soil in thinned, unthinned, and clear-cut conifer stands on two sites in the Oregon Coast Ranges. For all species, seedling emergence and survival were greater in thinned stands than in clearcuts or unthinned stands. In addition, emergence of salmonberry and salal was greater on mineral soil than on soil in which the organic layers were intact. After four years, height of salmonberry was greatest in the clearcuts, where it averaged 23 cm. Bigleaf maple and vine maple, which were heavily browsed in the clearcuts, reached their greatest height in the thinned stands, averaging 16 and 15 cm, respectively. Salal seedlings survived only in thinned stands and grew slowly, reaching a height of only 4–5 cm in 4 years. Seedling emergence and predation both were related to seed size. On both disturbed and undisturbed soil, vine and bigleaf maple, the species with the largest seeds, had the highest rates of emergence but also the highest rates of seed predation among the four species.

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Afin d'identifier les niches de régénération par semis de quatre arbustes et feuillus de la zone côtière de l'Orégon (ronce élégante (*Rubus spectabilis* Pursh), gaulthérie shallon (*Gaultheria shallon* Pursh), érable circiné (*Acer circinatum* Pursh) et érable à grandes feuilles (*Acer macrophyllum* Pursh)), les auteurs ont étudié la prédation des semences, l'émergence, la survie et la croissance de ces espèces sur des sols perturbés ou non, dans des peuplements éclaircis, non éclaircis et coupés à blanc, sur deux stations de la chaîne côtière de l'Orégon. Pour toutes les espèces, l'émergence des semis et leur survie étaient supérieures dans les peuplements éclaircis par rapport aux coupes à blanc ou aux peuplements non éclaircis. De plus, l'émergence de la gaulthérie shallon et de la ronce élégante était supérieure sur les sols minéraux par rapport aux sols où les couches organiques étaient intactes. Après 4 ans, la hauteur de la ronce élégante était la plus élevée dans les coupes à blanc avec une moyenne de 23 cm. L'érable à grandes feuilles et l'érable circiné, qui ont été broutés abondamment dans les coupes à blanc, ont atteint leur plus grande hauteur dans les peuplements éclaircis, soit des moyennes de 16 et 15 cm respectivement. Les semis de la gaulthérie shallon ont survécu seulement dans les peuplements éclaircis et ont poussé lentement, atteignant une hauteur de 4–5 cm en 4 ans. L'émergence des semis et la prédation étaient toutes deux reliées à la dimension des semences. Sur les sols perturbés ou non, les érables circinés et à grandes feuilles, les espèces avec les semences de plus fortes dimensions, présentaient les taux d'émergence les plus élevés mais aussi les plus forts taux de prédation des semences parmi les quatre espèces.

[Traduit par la rédaction]

Introduction

Hardwoods and shrubs are major components of coastal Oregon forest vegetation. They often form dense layers in the forest understory and rapidly respond to disturbance, and so they may delay or prevent the regeneration of conifers and other species. They are, however, structurally important within these forest ecosystems, providing food and cover for wildlife, modifying nutrient cycling (Fried et al. 1990; Perry et al. 1987), and probably affecting other processes as well.

Identifying the environments favorable for shrub and hardwood seedling establishment (that is, the seedling regeneration niches (Grubb 1977)) is critical for determining the dynamics of shrubs and hardwoods in stand development. How successfully a given species regenerates from seed apparently is related to successional stage (Oliver and Larson 1990). For some coastal Oregon hardwood and shrub species, successful regeneration seems to occur primarily on heavily disturbed sites such as clearcuts (Haeussler 1987), during the stem initiation stage of forest succession. For others, the probability of establishment appears to be greatest during self-thinning or commercial thinning of the conifer overstory and before a dense understory develops (Tappeiner et al. 1986; Fried et al. 1988; Alaback and Tappeiner 1991); that is, during the stem reinitiation stage.

The identification of a plant's regeneration niche requires examination of environmental variables that affect the plant's probability of establishment from seed. Familiarity with aspects of the plant's life cycle such as production and sur-

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vival of reproductive buds; flowering; seed maturation, predation, and dispersal; seed pool dynamics; germination; and seedling survival and growth is also important (Grubb 1977; Harper 1977; Wilson 1983; Zasada et al. 1991).

In this study, we examined seedling regeneration of four species that are prevalent in coastal Oregon forests: salmonberry (*Rubus spectabilis* Pursh), salal (*Gaultheria shallon* Pursh), vine maple (*Acer circinatum* Pursh), and bigleaf maple (*Acer macrophyllum* Pursh). All four of these species are capable of survival and growth in low-light environments and are classified as stress tolerators according to Grimes (1979). Inherent differences among the species, however, may result in their having different capacities for regeneration from seed. For example, their seed sizes range from large for bigleaf maple (7100 seeds/kg) to very small for salal (6.6×10^6/kg). Seed dormancy patterns also differ among the four species: salal seeds have little or no dormancy, while salmonberry and vine maple seeds have deep dormancy and may remain in a buried seed pool for many years. Seedling growth varies as well. For bigleaf maple, growth is relatively rapid (first-year growth can be as much as 2 m under ideal conditions), whereas salal growth is very slow (even under ideal conditions seedlings are less than 2 cm tall after one growing season). Although all four of the species in our study also sprout following disturbance and are present as clones in clearcuts, the clones may be killed or greatly reduced in vigor and size under dense conifer canopy during the stem exclusion stage of stand development (Huffman 1992; Tappeiner et al. 1991). Thus, in coastal Oregon forests, seedling establishment is an important aspect of understory development in many stands.

To help identify the seedling regeneration niches of these species, we compared each species' seed predation rates and seedling emergence, survival, and height growth in three stand types (a clearcut, a dense 40- to 50-year-old conifer stand, and a thinned conifer stand of the same age) on two sites of the Coast Ranges in the *Tsuga heterophylla* (Raf.) Sarg. zone (Franklin and Dyrness 1973). These three stand types represent the stem initiation, stem exclusion, and stem reinitiation stages of forest development, respectively, as outlined by Oliver and Larson (1990). In addition, we examined the effect of substrate type (mineral soil or undisturbed forest floor) on the four species' seedling regeneration capabilities.

Study sites

We chose two study sites in the Oregon Coast Ranges, both in the *Tsuga heterophylla* zone (Franklin and Dyrness 1973). Cape Creek (CCR) is about 12 km from the ocean and is in the moist oxalis/sword fern association; Randall (R) is about 30 km from the ocean and is in the drier salal/vine maple association. All four of the species we studied were part of the flora at both sites. Both sites included (*i*) a dense, 40- to 50-year-old conifer stand with 50 to 58 m^2/ha basal area and less than 5% understory cover; (*ii*) a conifer stand of the same age, thinned 3–5 years previously to 30–36 m^2/ha basal area and with about 10–15% understory cover mainly from the establishment of new seedlings; and (*iii*) a 2-year-old clearcut. Fish-eye photographic estimates of average percent visible sky were 21 and 22% in unthinned stands, 47 and 32% in thinned stands, and 93 and 90% in clearcuts at R and CCR, respectively (Chan et al. 1986).

Methods

Plot establishment

In the fall of 1987, we established 40 seedling exclosures and 40 adjoining unprotected plots in each of the thinned and unthinned stands, and 20 of both in each clearcut. The exclosures, which were used to protect the sown seeds from predators, were circular, wire-mesh (0.2×0.2 cm) cages, 75 cm in diameter, open at the bottom, covered on top, and set 10–15 cm into the ground. The cages extended 15 cm above ground, well above the tops of 1- to 2-year-old seedlings. The unprotected plots were equal in surface area and shape to the exclosures. In half the exclosures and adjoining unprotected plots, we left the forest floor undisturbed. In the other half, we exposed the mineral soil by carefully removing the organic layers, which were generally less than 1 cm thick. In the clearcuts, only mineral soil plots were used because no undisturbed forest floor existed. In July 1988, the first summer after the seed of all four species was sown, the wire tops were removed from the exclosures containing salal and bigleaf maple. Because a preliminary study had shown that vine maple and salmonberry seedling emergence continued into the second summer after sowing, tops were not removed from the exclosures surrounding these species until July 1989.

Seed collection and sowing

Seeds were collected in 1987 at the time of natural dispersal for each species (salmonberry in June, salal in September, and bigleaf and vine maple in October) and stored at 2–3°C until the November sowing. To isolate the salmonberry seeds, we treated the berries in a blender for 20–30 s and then removed the pulp, which was lighter than the seed, by flotation in water. The salal capsules (pseudoberries) were dried at 20–22°C for 3–4 days, and then the fleshy material of the fruit was separated from the seeds by gentle grinding in a mortar and pestle followed by sieving and air blowing to remove lighter, nonseed material. Bigleaf and vine maple samaras were sown without dewinging.

For both substrate types within each stand, each of the four species was sown in five replications in both the exclosures and the unprotected plots. Prior to sowing, filled-seed percentages of all species were determined with a cutting test and, for bigleaf maple and salal, confirmed by a subsequent germination test (Dimock et al. 1974; Zasada et al. 1990). (Germination tests were not conducted for salmonberry and vine maple because exploratory field and nursery bed studies had indicated that cutting tests were sufficiently reliable for estimating viability of fresh seeds for these species.) Based on our tests, the estimated numbers of sound seeds sown per plot were 400 for salal, 150 for vine maple and bigleaf maple, and 300 for salmonberry. Preliminary field tests had shown that sowing in these numbers would produce sufficient seedlings in all test environments to study each species' emergence and survival for 3–4 years.

All of the salal and salmonberry seed was washed into the forest floor within 1 week of sowing. About half of the much larger vine and bigleaf maple seed remained partially exposed on top of the undisturbed or mineral soil.

Seedling measurements and data analysis

We monitored seedling emergence by counting the total number of seedlings per exclosure every 2 weeks from February to July 1988 and then once each in August and October from 1988 to 1991. We noted all species that emerged in the exclosures and unprotected plots, not just the species that were sowed in them. For each observation date through October 1990, we calculated percent seedling emergence for each exclosure by dividing the number of seedlings present by the estimated number of seeds sown. Then, at the final tally in October 1991, we calculated percent seedling survival for each exclosure by dividing the number of seedlings present by the maximum number of seedlings counted on the plot. In October 1991 we also measured seedling heights and calculated the mean height for each plot, and we estimated seed predation rates for each species by comparing seedling emergence in the exclosures and in the adjoining unprotected plots.

We analyzed the emergence, survival, height, and seed predation data for each species separately, using analysis of variance and a factorial design. We tested the null hypotheses that seedling emergence, survival, size, and seed predation did not differ by site, stand type (thinned, unthinned, or clearcut), or substrate type (mineral soil or undisturbed). In cases where significant site × treatment interactions existed, we analyzed the data separately for each site.

Results

Emergence, survival, and height

Overstory density and substrate type both affected seedling emergence, survival, and height growth. The nature of the effects, however, differed among species and sometimes varied between the two sites. Except for occasional salmonberry seedlings, we noted no natural seedlings of these four species emerging within or among the exclosures and unprotected plots.

Salmonberry

Emergence was consistently greater on mineral soil than on undisturbed soil in both thinned and unthinned stands, significantly so at R and in the unthinned stand at CCR ($p \leq 0.01$–0.05) but not in the thinned CCR stand ($p \leq 0.10$) (Fig. 1). On disturbed soil at R, significantly ($p \leq 0.01$) more salmonberry seedlings emerged in the thinned stand than in the unthinned stand or clearcut. At CCR, emergence on disturbed soil was significantly ($p \leq 0.05$) greater in the clearcut and thinned stand than in the unthinned stand. A considerable proportion of seedling emergence occurred during the second year in the thinned and unthinned stands (between 13 and 72% of total emergence on plots at CCR and between 21 and 63% at R). In contrast, most (over 95%) emergence in the clearcuts occurred during the first year.

Average seedling survival after 4 years was significantly ($p \leq 0.007$–0.01) greater in thinned stands than in both unthinned stands and the clearcut at CCR (Fig. 2). Among plots in the same stand and substrate type, however, survival varied greatly; for example, it ranged from 0 to 45% for plots on undisturbed soil in thinned stands. Thus, we could detect no significant differences in seedling survival related to soil disturbance, even though there was consistently greater average survival on disturbed soil.

After 4 years, salmonberry seedlings were the largest of the four species; their height averaged 23 cm in the clearcuts and 16 cm in the thinned stands. Browsing was common in the clearcuts and consequently the height growth of salmonberry seedlings in this environment is potentially greater than our data indicate.

Salal

Salal seedling emergence was erratic, generally occurring on only two or three mineral-soil plots in each stand type. In the thinned stands at both R and CCR and in the unthinned stand at R, emergence was significantly ($p \leq 0.001$) greater on mineral soil (31–80%) than on undisturbed soil (4–35%) (Fig. 1). Emergence was also significantly ($p \leq 0.01$) greater in these three stands than in the clearcut at either site (0–1%).

Salal survival was comparatively low (Fig. 2). Seedlings survived only on two or three mineral-soil plots in each of the thinned stands and averaged 18% at R and 19% at CCR. Salal seedlings were the smallest of the four species, averaging only 4–5 cm in height after 4 years.

Vine maple

Vine maple seedling emergence was significantly ($p = 0.004$) greater in the thinned and unthinned stands than in the clearcut at both sites (Fig. 1). At R, emergence was greatest in the unthinned stand; at CCR, it was greatest in the thinned stand but not significantly greater than in the unthinned stand.

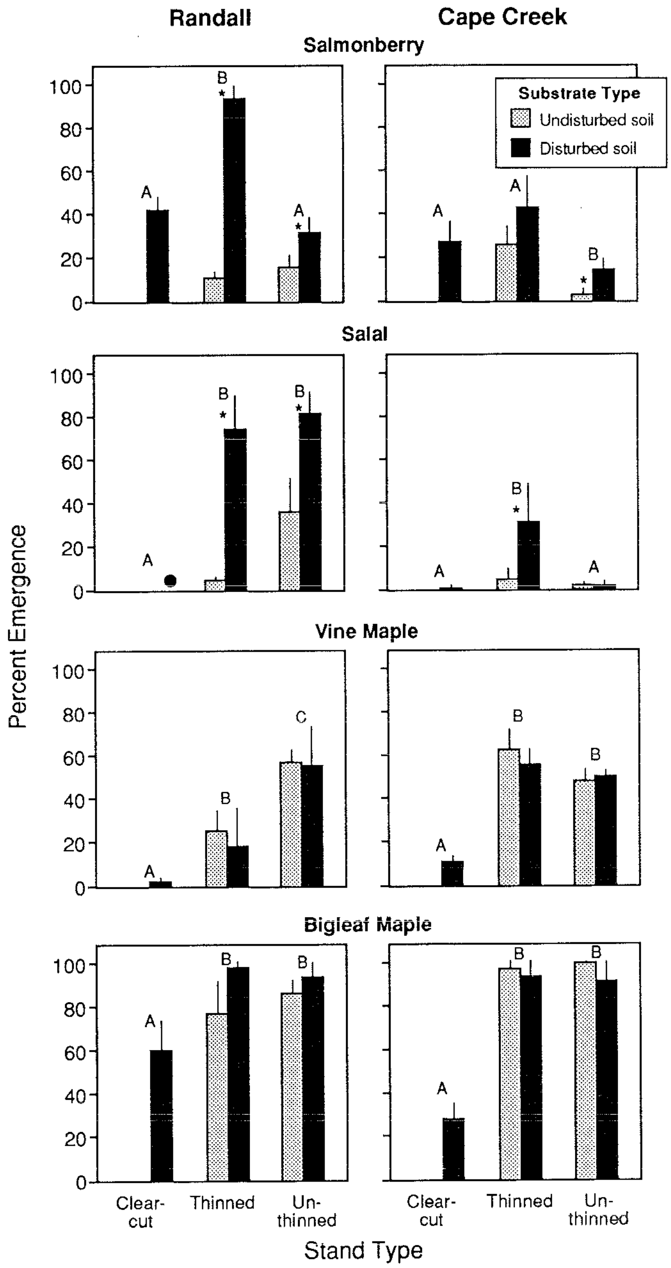

FIG. 1. Average seedling emergence within exclosures, by site, stand, and substrate type. (The clearcuts contained no undisturbed plots.) Emergence was calculated as maximum number of seedlings observed divided by number of seeds sown. For vine maple and salmonberry, which emerged over several growing seasons, the data for all growing seasons are combined. Vertical bars represent standard errors. ●, no emergence. For any given species at either site, different letters above the bars representing the various stand types indicate a significant ($p < 0.05$) difference in seedling emergence among the stand types (in disturbed and undisturbed soils combined). *, for a given stand type, emergence on disturbed and undisturbed soils within that stand type was significantly different.

Second-year emergence was consistently greater than first-year emergence, averaging 81, 88, and 69% of total emergence in the unthinned, thinned, and clear-cut stands, respectively. Third-year emergence represented from 0 to 5%

of the total. There was no significant effect of soil disturbance on seedling emergence.

Vine maple survival was significantly ($p < 0.001$) greater in the clearcut and the thinned stand than in the unthinned stand at CCR (no seedlings survived in the unthinned CCR stand). Survival at R was not significantly ($p < 0.694$) different in the thinned and unthinned stands but was significantly ($p < 0.05$) greater in both of these stand types than in the clearcut (Fig. 2). As with seedling emergence, substrate type did not significantly affect seedling survival.

Vine maple seedlings were browsed in all stands at both R and CCR, and after 4 years, their height averaged 15 cm in the thinned stands, 10 cm in the clearcuts, and 7 cm in the unthinned R stand.

Bigleaf maple

Bigleaf maple was the first species to germinate, with germination activity observed in late February 1988. All emergence occurred by July 1988. Percent emergence was significantly ($p \leq 0.02$) greater in the thinned and unthinned stands than in the clearcuts at both R and CCR (Fig. 1). Also, at both sites, seedling survival was significantly ($p \leq 0.001$) greater in the thinned stands than in the unthinned stands. At R, survival in the clearcut was significantly ($p \leq 0.001$) less than in the thinned stand, but at CCR there was no difference in survival rates between these two stand types (Fig. 2). As with vine maple, substrate type had no effect on either emergence or survival. Also like vine maple, bigleaf maple seedlings were heavily browsed, especially at CCR. Four-year heights averaged 16 cm in the thinned stands, 12 cm in the clearcuts, and 6 cm in the unthinned R stand.

Seed predation

Bigleaf and vine maple seedling emergence was only 0–4% on the unprotected plots, significantly ($p < 0.001$) less than in the exclosures. No vine maple seedlings emerged the second or third year on unprotected plots. At the end of the 4-year study period we found no ungerminated, filled bigleaf or vine maple seed remaining on any of the unprotected plots on which they were sown, and thus we attribute the lack of emergence on these plots to predation. In contrast, we found no significant differences in salmonberry and salal emergence between the unprotected plots and the exclosures, although in the thinned CCR stand, salal emergence on unprotected plots was only about 40% of that in the exclosures.

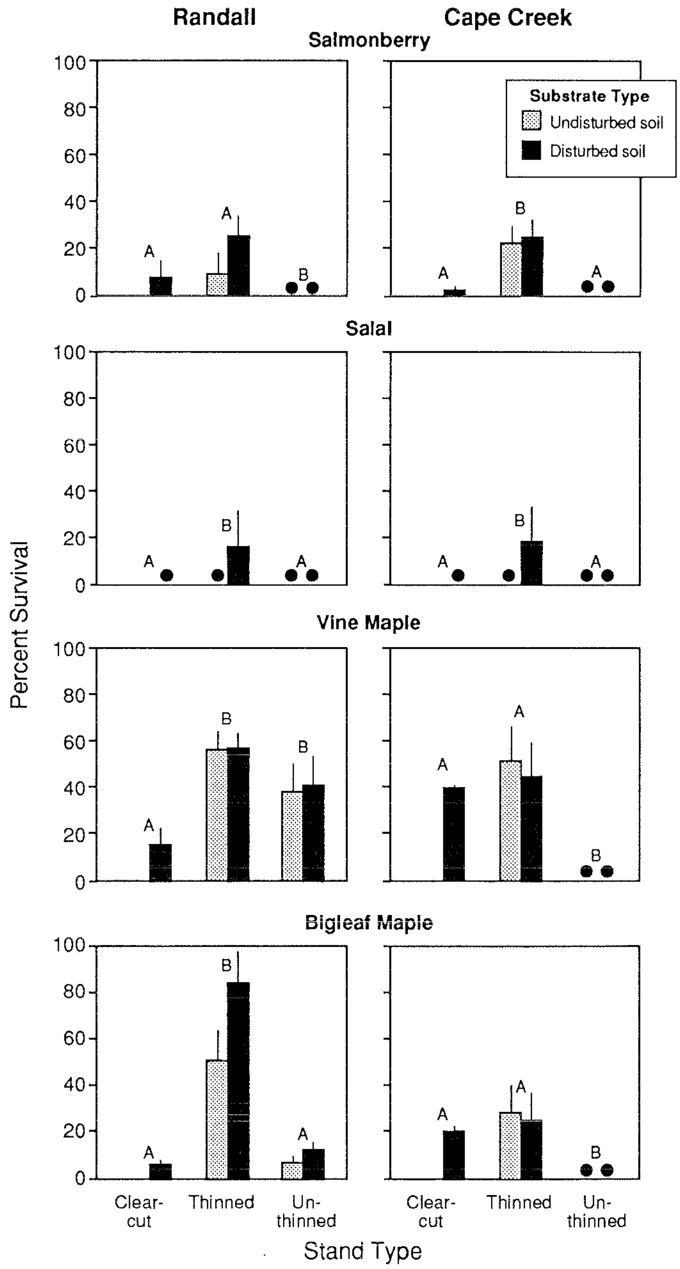

FIG. 2. Average 4-year seedling survival by site, stand, and substrate type. (The clearcuts contained no undisturbed plots.) Survival was calculated as number of seedlings present after four growing seasons divided by total number of emerged seedlings. Vertical bars represent standard errors. ●, survival was less than 0.5%. For any given species at either site, different letters above the bars representing the various stand types indicate a significant ($p < 0.05$) difference in survival among the stand types. Substrate type did not significantly affect survival in any of the stands.

Discussion

Our experimental results indicate that for each of the four species studied, a particular successional stage is most conducive to seedling emergence and survival. Bigleaf maple, vine maple, and salal all performed best in commercially thinned stands, the study environment that represented the stem reinitiation stage; that is, the stage that occurs after the forest canopy is reopened (by self-thinning, windthrow, or commercial thinning, for example) and before a dense understory of shrubs, herbs, hardwoods, or conifers develops. Other studies on bigleaf maple (Fried et al. 1988) and vine maple (O'Dea 1992) reported similar findings for these two species. Salmonberry also is readily established from seed at the stem reinitiation stage, but as demonstrated by its performance in the clearcuts, it also appears well suited for establishment in the stem initiation stage. Our findings also suggest that exposure of mineral soil on the forest floor enhances salal and salmonberry establishment but that the presence of organic layers on the forest floor has little or no effect on the establishment of vine and bigleaf maple, perhaps because of their larger seed. Finally, we found that seed predation apparently is a factor in seedling establishment of vine and bigleaf maple but not of salal or salmonberry.

In the evaluation of our study results, several issues arose that merit further comment and investigation. These issues are summarized in the following paragraphs.

Environments studied

To determine the seedling regeneration niches of the four species we studied, we sampled the general environments created by overstories representing various successional stages. There are environments within these overstory types that we did not sample, however. For example, within a clearcut, shade from sprouting shrubs and hardwoods may create an environment similar to that found in thinned stands with exposed mineral soil. Also, within thinned and unthinned conifer stands, environments below vine maple clones and dense salmonberry or salal covers, which we did not sample, would probably preclude seedling establishment. Finally, decomposing logs on the forest floor have been identified as suitable sites for western hemlock regeneration (Christy and Mack 1984; Harmon and Franklin 1989) and for salal regeneration as well (Huffman 1992).

The results suggest that seedling establishment may occur just as readily on interior sites (R) as on coastal sites (CCR), where the plant associations (Franklin and Dyrness 1973) indicate a moister environment. Seedling establishment seems to be more related to stand density and other variables than to the general environment of the site (Fig. 2). For example, except for vine maple at R, seedling survival was poor for all species in the dense, unthinned stands. Also, although survival of bigleaf maple was lowest at CCR, it was nearly the same at both sites until the third year, when there was considerable mortality from browsing at CCR. Studies like this would have to be replicated at several coastal and interior locations, for several years, to determine whether seedling establishment rates of these four species differ on coastal and interior sites.

Regeneration niche versus growth niche

Environments that favor seedling establishment may be different from those that are optimal for continued growth. For example, although salmonberry survival was greater in thinned stands than in clearcuts, the salmonberry seedlings that survived in the clearcuts were larger after 4 years than those in the thinned stands. On the other hand, bigleaf and vine maple seedlings grew as well for 4 years in thinned stands, where survival was highest, as in the more open environment of the clearcuts, which might be expected to be more favorable for growth.

Seed size

Seed size appeared to have an effect on seedling establishment in our study. In the exclosures, the larger seeded species, bigleaf maple and vine maple (7100–9300 seeds/kg), had higher rates of emergence and survival than the smaller seeded salmonberry (315 000 seeds/kg) and salal (6 600 000 seeds/kg), and they emerged equally well on disturbed and undisturbed soil. However, seed predation rates were also higher for the maples than for the smaller seeded species. Similarly, on a variety of southern Oregon sites, tanoak (*Lithocarpus densiflorus* (Hook. and Arn.) Rehd.), a heavy-seeded hardwood, had substantially higher rates of seedling emergence and survival, but also of predation, than the lighter seeded Pacific madrone (*Arbutus menziesii* Pursh) (Tappeiner et al. 1986). Also, in a study conducted on boreal forest sites, larger seeded species had higher germination and survival rates than smaller seeded species (Zasada et al. 1983).

For the smaller seeded species, seed size appeared to affect emergence on the undisturbed plots adversely. The greater emergence of salal and salmonberry seedlings on mineral soil compared with undisturbed plots was perhaps due to higher light and temperature levels on mineral soil, as well as to the small seeds' relatively low stored energy, which may have reduced the seedlings' ability to emerge above the undisturbed forest floor.

The lower rates of salal and salmonberry emergence on undisturbed plots may also have been due to seed predation by invertebrates. Haeussler (1987) has shown that on sites similar to ours, invertebrate and fungal predation of red alder (*Alnus rubra* Bong.) seed was much higher on undisturbed plots than on mineral soil. For example, insects and fungi damaged 60 to 65% of the seed in undisturbed soil compared with only 10 to 30% of the seed in mineral soil.

Seed dormancy

A large proportion (>70%) of the vine maple seedlings emerged the second year after sowing. We sowed vine maple seed during the period of natural seed dispersal, so it is unlikely that the delayed germination was artificially imposed. In two pilot studies, we also noted a 1-year delay in vine maple germination. In one of the studies, we sowed over 1200 seeds in a clearcut and a thinned stand. Over 80% of the total emergence occurred the second year after sowing; less than 2% occurred the third year. Similarly, in the other pilot study, over 80% of the vine maple seed planted in a nursery bed germinated the second year.

In the thinned and unthinned stands at CCR and R, salmonberry seedlings emerged both the first and second years after sowing. Other studies have also reported a seedbank strategy for salmonberry (Ruth 1970; Barber 1976; Maxwell 1990). In the clearcuts, significant salmonberry emergence occurred only in the first year after sowing. Possibly, the layer of grasses and herbs that developed throughout the clearcuts in year 2 inhibited emergence of those seedlings that may have germinated after a 1-year dormancy period.

Bigleaf maple and salal seeds exhibit little dormancy and germinate rapidly and completely after short periods of stratification. It appears unlikely that seeds of these species are as adapted for storage in a seedbank as salmonberry and to a lesser extent vine maple (Sabhasri 1961; Schopmeyer 1974; Zasada et al. 1990; Huffman 1992).

Management implications

Our results suggest that seedlings of the four shrub and hardwood species we studied are not likely to provide competition to conifer seedlings planted in clearcuts or other disturbed sites. Seedling emergence and survival were low for all four species in clearcuts, and even though the height of surviving salmonberry seedlings was greater in clearcuts than in thinned stands after 4 years, these seedlings were only about 10–20% as tall as the 4-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings (which were 100–200 cm in height) present on the site.

Commercial thinning seems to favor the establishment of these four species from seed and also favors the development of a vigorous understory with the potential for vigorous resprouting following fire, clear-cutting, windthrow, or other disturbances to the overstory. Although vegetative reproduction was not examined in this study, other research suggests that thinning also encourages clonal expansion of salal (Huffman 1992) and salmonberry (Tappeiner et al. 1991), as well as layering of vine maple (O'Dea 1992). Thus, if salal, salmonberry, and vine maple clones are present in a stand, vegetative reproduction rather than seedling regeneration will probably play the greater role in establishing a dense understory of these species following thinning. However, the dense overstory that develops in many young stands in the Oregon Coast Ranges prior to thinning tends to kill clones present at the stem initiation stage. Seedling regeneration therefore is likely to be a major mechanism of understory establishment in many thinned stands in western Oregon forests.

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